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REVIEW ARTICLE

Timberlines of the Greek high mountains: status quo at the turn of the millennium

Robert Brandes[1*], Anastasia Christopoulou[2,3]

[1]*Geographer and independent consultant, Geuschmidstr. 8, D-90480 Nuernberg, Germany*
[2]*National and Kapodistrian University of Athens, Department of Biology, Section of Ecology and Systematics, Panepistimiopolis, 15784 Athens, Greece*
[3]*Biodiversity Conservation Lab, Department of Environment, University of the Aegean, 81100 Mytilene, Greece*

Corresponding author: Robert Brandes (dr-robert-brandes@t-online.de)

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Abstract

The present review article provides an overview about the timberlines of the Greek high mountains. It informs about the existing tree species and about the altitude, physiognomy and dynamics of the timberline ecotones. Subsequently, it gives an interpretation of the human influence and the geo-ecological factors, which may have caused the altitudinal limit of tree growth in Greece. A latitudinal and local change in timberline-forming tree species creates high heterogeneity between the research areas and makes this their most remarkable feature. Moreover, in Greece there is no rise in timberline altitude from north to south. In some areas, fir-dieback causes a local decline in timberline altitude, which is the predominant dynamic process. An anthropogenic depression of the forest line is certainly common. Yet, a natural forest cover reaching up to the peak zones of the Greek high mountains is unthinkable. The identified timberline-forming factors and the prevailing site conditions speak against this. In accordance with the Mediterranean climate regime, it is obvious that not only the climatic conditions of winter (frost, snow) determine the limits of tree growth. The (macro- and micro) climatic impacts of summer (drought, high insolation) play a highly important role as well. Against this background, the climate-ecological hindrances to the establishment of trees, i.e. the germination and the survival of seedlings, are identified as key-factors for understanding the Hellenic timberlines ("regeneration hypothesis"). Against the background of global warming, suggestions for further research on the ecology and dynamics of the Greek high mountain timberlines are provided.

Keywords

Greece, Mediterranean, Mt. Olympus, treeline, timberline dynamics, climate change

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Introduction

Mountain timberlines have been subject to global research, in mountain areas with very different climatic conditions, from tropical to arctic. Detailed regional studies are required to understand the ecology of timberline ecotones because the same phenomenon, i.e. the transition zone between the closed forest and the treeless high mountain vegetation, can have a variety of causations, which lead to different geo-ecological types of timberlines (Höllermann, 1978; Arno, 1984; Holtmeier, 2003).

The Hellenic peninsula features various mountain ranges higher than 2.000 m a.s.l., which clearly fulfill the definition of "high mountains" (Rathjens, 1982). Yet, merely one monography has provided detailed and comprehensive information about the timberlines of the Mediterranean-type high mountains on the Greek mainland (Brandes, 2007). Since then only a few timberline-focused, regional studies have followed (e.g. Zindros et al., 2020, Beloiu et al., 2022, Sidiropoulou et al., 2022).

The present review paper is based on the findings of Brandes (2007) and on more recent visits of the authors' team to the research areas. It has the target to give a general overview about the status quo of the Greek timberlines at the turn of the millennium. At the same time it provides a valuable benchmark for the detection of future developments that could be caused by changes in land use (recessive grazing regime) and by climate-ecological factors. Plants in ecotones are often growing under conditions of physical and biotic stress (Delcourt, Delcourt, 1992). Therefore, timberline ecotones are supposed to mirror climate change effects relatively early. This has rightly made them a focal point of ecological research all over the world, for decades (Hansen et al., 1992; Wieser et al., 2009).

The research areas

Fig. 1 shows the 11 research areas on the Greek mainland. Mt. Olympus and Mt. Smolikas (at ca. 40°03'N) mark the northern, Mt. Taygetos (at ca. 36°57'N) the southern geographical limit of the study area. From their foothills up to the highest altitudinal zones, the vegetation of these high mountains belongs to a genuine Mediterranean type (Voliotis, 1976; Brandes, 2007). This aspect distinguishes the research areas from the mountains further north on the Balkan Peninsula, which are part of a Centraleuropean-Balkan vegetation type (Horvat et al., 1974).

Geologically limestones, dolomite and marble prevail at the Greek timberline ecotones, forming a mostly karstic substrate. Only Mt. Smolikas is a distinct exception. There, serpentinite (a metamorphic ophiolite) forms a non-karstic bedrock, which is nonetheless a very dry substrate for plants. The ultrabasic chemistry of serpentinite allows only a very sparse plant cover and leads to a landscape dominated by lithosoils (Horvat et al., 1974). Serpentine (ophiolithic) substrate hosts a distinctive flora, with numerous endemic species (Strid, 1995; Stevanović et al., 2003).

This geological situation, together with the predominantly steep terrain, usually causes shallow soils or entirely rocky substrates in the altitudinal zone between the oromediterranean forests and the treeless peaks. In some areas erosion, produced by

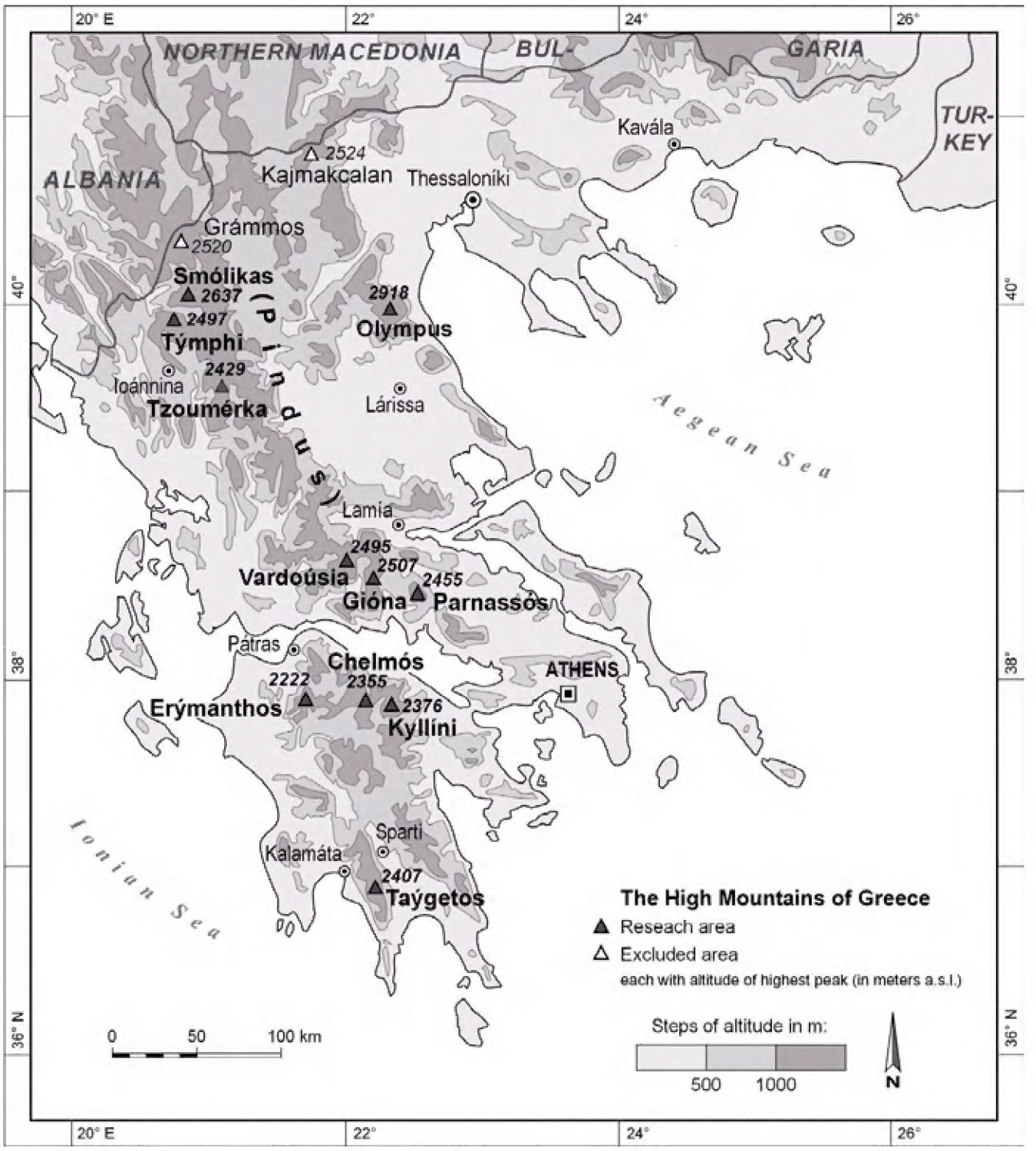

Fig. 1. The research areas (Brandes 2007, modified)

grazing, plays an additional role. Thus, in an ecological sense, generally unfavorable edaphic conditions are a characteristic feature of all the Greek timberlines and they strongly contribute to the dominance of dry site conditions. At large, any plant life existing beyond the forest line is exposed to a great risk of water deficiency, since water supply stands in a very direct temporal relation to precipitation.

Reliable long-term climatic data from very high elevations are regrettably missing in Greece, despite the numerous mountain areas and their important role for the water balance of the country.

The basic setting of the yearly rainfall pattern still shows the typical Mediterranean summer incision, which is more pronounced in the south than in the north of the Hellenic peninsula (Bolle, 2003). In winter there is generally high precipitation, often in the form of snowfall. The snow cover period at the timberline altitudes

can last from December to March, while snowfields in concave relief can stay until May (Brandes, 2007; Christopoulou et al., 2022a). During the vegetation period of trees, i.e. from springtime to autumn, precipitation quantities are unsteady and therefore become a paramount ecological factor. Dendroecological and dendroclimatological studies near the timberlines of Mt. Taygetos (Brandes, 2007; 2009) and in the Northern Pindus National Park (Klippel et al., 2017; 2018; Esper et al., 2021; Christopoulou et al., 2022a) have revealed, that even in the high mountains there is an extremely strong variability in precipitation, on a year-to-year basis as well as on a decadal time frame, including the occurrence of severe drought years. Apart from the southwards increasing summer drought, also the immediate geographical closeness of some mountain areas to the sea plays an important role. There, local sea-land wind systems bring clouds, fog and precipitation to the high elevations (most obvious on Mt. Olympus and Mt. Taygetos) and cause a general hygric preference of the windward exposed mountain flanks (Schreiber, 1998). For this reason Mt. Taygetos is the southernmost, but not the driest mountain range on the Peloponnese. In the northern Pindus (Mt. Smolikas, Mt. Tymphi) a different reason seems to bring moisture, even in the summer months. There, the big mountain mass leads to convective processes, i.e. to frequent and heavy thunderstorms ("Merriam effect"; Richter, 1996). This becomes readable in a remarkably high number of lightning damages on the trunks of the multi-century old Bosnian pines (*Pinus heldreichii* Christ) growing in the area. The nomenclature of taxa follows POWO (2024).

The thermic conditions at the timberlines (in altitudes > ca. 1.700 m a.s.l.) differ much from the lowlands, i.e. the summer months are warm, but not as hot as in the plains. Nevertheless, given that the intensity of insolation increases with altitude and cloudless summer days are frequent, soil surfaces at high altitudes can heat up considerably. In winter, frost rules in the high mountains of Greece and temperatures around -20 °C have been documented for the peak zones (Hagedorn, 1969; Athanasiadis, 1974).

In brief, the climate-ecological situation at the Greek timberlines can be described best as a very strong seasonal contrast of dry conditions (lack of precipitation, high insolation, high soil surface temperatures, wind influence) prevailing in summer. On the other hand stand harsh winter conditions, i.e. snow cover and frost impact. Spring and autumn are only short periods between these extremes, with moderate temperatures and great variance in precipitation (Brandes, 2007).

The timberlines: an overview

In order to describe and define any timberline ecotone it is highly important to clarify the applied terminology precisely (Körner, 1998; Holtmeier, 2003), especially since slightly different definitions are given from different authors. According to Heikkinen et al. (1995) timberline is the zone of transition from boreal forest to treeless tundra in the polar regions, or from montane forest to the alpine belt on mountains. It corresponds to a temperature limit in summer, or rather, a limit in heating degree days (i.e. the length of growing season), reached either by elevation on mountains or by high

latitude. Jørgensen (2009) and Körner (2012) describe timberline, as the line below which trees form a forest with a closed canopy. Timberline can be lower than the tree line which is the edge of a habitat at which trees are capable of growing. Treeline is found at high elevations and high latitudes. Beyond that edge trees cannot tolerate the environmental conditions (usually low temperatures, extreme snowpack, or associated lack of available moisture) (Elliott-Fisk, 2000). The treeline is the elevational limit of trees and is widely considered to be a sensitive indicator of environmental change (Aakala et al., 2014). The terminology used for timberline in this article is shown in Fig. 2. Of course it must be kept in mind that any definitions of vegetation limits are per se problematic, since any natural boundaries are in reality transition zones (Armand, 1992).

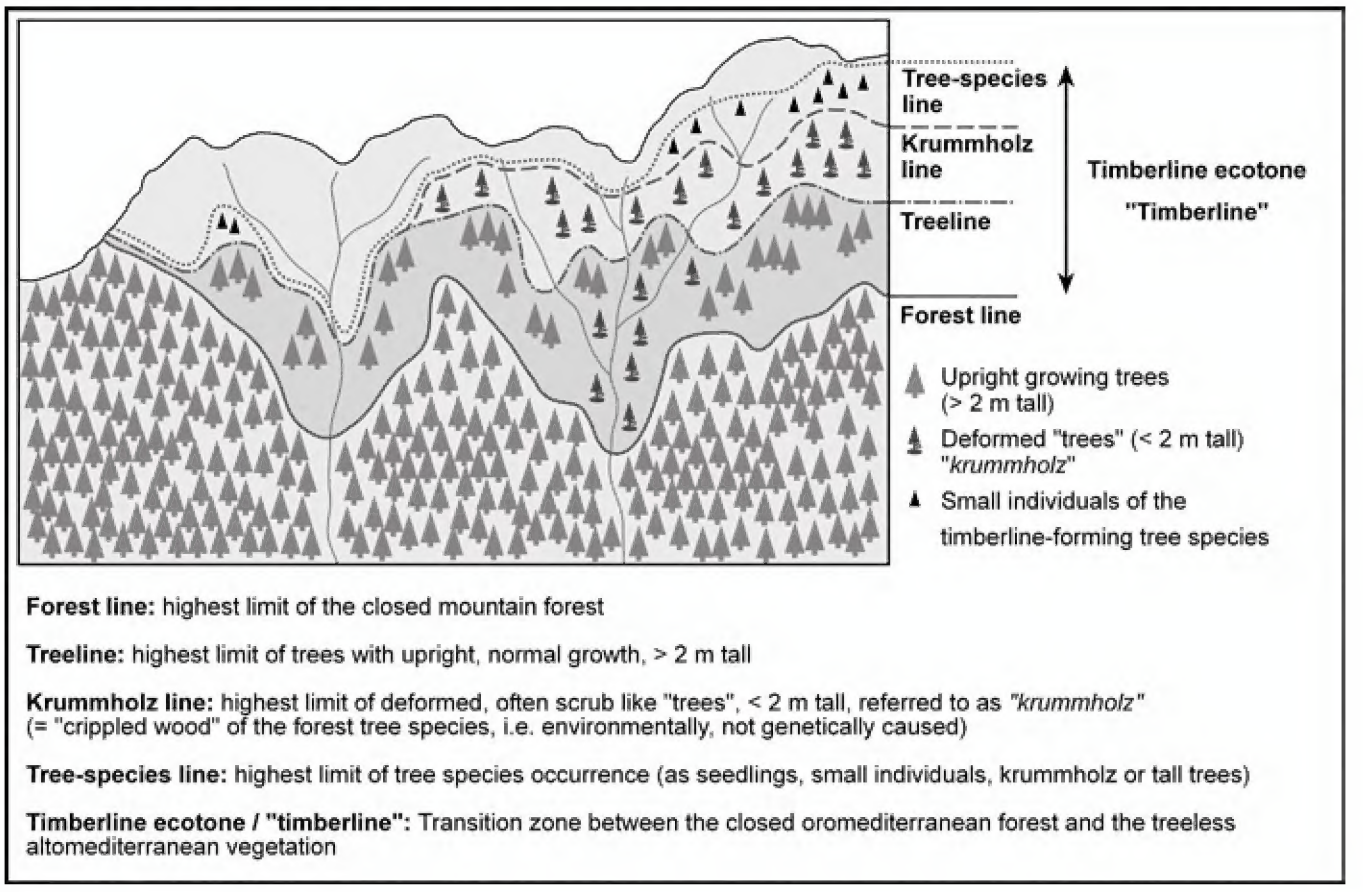

Fig. 2. Timberline terminology (Brandes 2007, modified)

It is important to note, that in Greece no genetically predetermined "true" krummholz (= "subalpine scrub") exists, such as *Pinus mugo* Turra, which is widespread in European high mountains (e.g. Alps, Carpathians, Dinaric Alps, Pirin and Rila mountain; Holtmeier, 2003). In Mediterranean Greece any "*krummholz*" is an environmentally induced phenotype of the forest tree species. Hence, stunted growth forms are clear evidence of harsh environmental influences preventing trees from growing to their normal, upright habitus.

Nanophanerophytes are represented at the Greek timberlines by *Juniperus oxycedrus* L. and *Juniperus communis* var. *saxatilis* Pall.. In a physiognomic sense these prostrate junipers are bushes, which hardly get higher than 1 m, but no krummholz. Also, they do not form belts, like *Pinus mugo*, but appear only scattered.

Based on detailed single studies of each research area (Fig. 1) by Brandes (2007), Fig. 3 gives a simplified, schematic overview on the timberlines of the Hellenic high mountains. It becomes obvious that they are characterized by high heterogeneity within a rather small geographical area. Fig. 4 gives an optical impression of this fact.

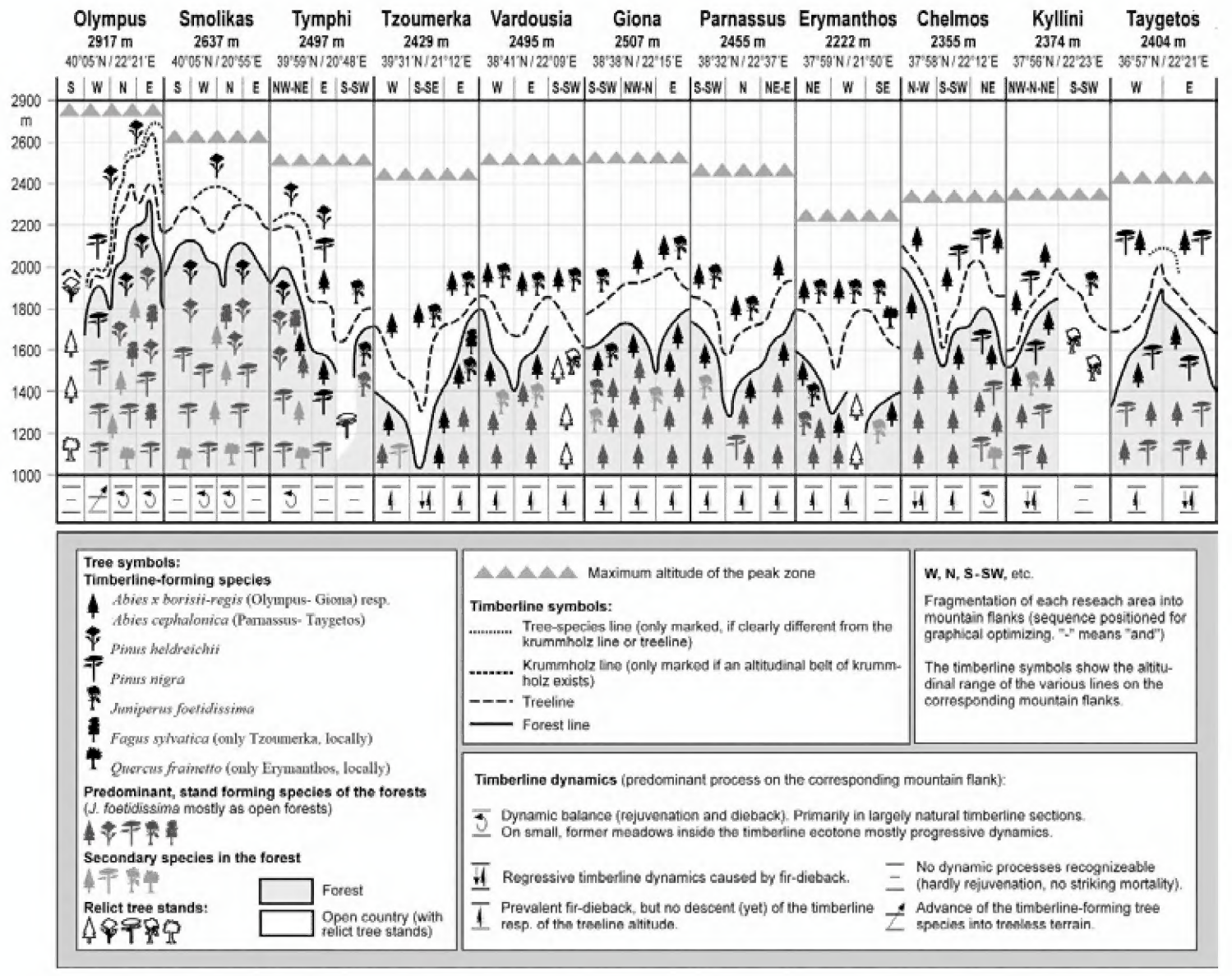
Olympus 2917 m 40°05'N / 22°21'E
Smolikas 2637 m 40°05'N / 20°55'E
Tymphi 2497 m 39°59'N / 20°48'E
Tzoumerka 2429 m 39°31'N / 21°12'E
Vardousia 2495 m 38°41'N / 22°09'E
Giona 2507 m 38°38'N / 22°15'E
Parnassus 2455 m 38°32'N / 22°37'E
Erymanthos 2222 m 37°59'N / 21°50'E
Chelmos 2355 m 37°58'N / 22°12'E
Kyllini 2374 m 37°56'N / 22°23'E
Taygetos 2404 m 36°57'N / 22°21'E
2900 m
2600
2400
2200
2000
1800
1600
1400
1200
1000
Tree symbols:
Timberline-forming species
Abies x borisii-regis (Olympus- Giona) resp.
Abies cephalonica (Parnassus- Taygetos)
Pinus heldreichii
Pinus nigra
Juniperus foetidissima
Fagus sylvatica (only Tzoumerka, locally)
Quercus frainetto (only Erymanthos, locally)
Predominant, stand forming species of the forests
(J. foetidissima mostly as open forests)
Secondary species in the forest
Relict tree stands:
Forest
Open country (with relict tree stands)
Maximum altitude of the peak zone
Timberline symbols:
Tree-species line (only marked, if clearly different from the krummholz line or treeline)
Krummholz line (only marked if an altitudinal belt of krummholz exists)
Treeline
Forest line
W, N, S-SW, etc.
Fragmentation of each reseach area into mountain flanks (sequence positioned for graphical optimizing, "-" means "and")
The timberline symbols show the altitudinal range of the various lines on the corresponding mountain flanks.
Timberline dynamics (predominant process on the corresponding mountain flank):
Dynamic balance (rejuvenation and dieback). Primarily in largely natural timberline sections. On small, former meadows inside the timberline ecotone mostly progressive dynamics.
Regressive timberline dynamics caused by fir-dieback.
No dynamic processes recognizeable (hardly rejuvenation, no striking mortality).
Prevalent fir-dieback, but no descent (yet) of the timberline resp. of the treeline altitude.
Advance of the timberline-forming tree species into treeless terrain.

Fig. 3. Schematic overview of the timberlines of the Hellenic high mountains (Brandes 2007, modified)

The timberline-forming tree species

Five tree species belonging to three genera of conifers dominate the Greek timberlines. There is a conspicuous latitudinal change of these timberline-forming tree species. Moreover, in most of the mountain areas also an additional, local change of tree species occurs (between mountain flanks or single slopes), which depends mostly on exposition. Strong exposition contrasts are a typical feature of subtropical high mountains and often go along with a change in tree species, since the sunny slopes there are not only warmer, but also drier (Holtmeier, 2003).

Pinus heldreichii (Bosnian pine) a Tertiary relict, endemic to the Balkans and southern Italy, rules on Mt. Olympus, on Mt. Smolikas, and on the northern flank of Mt. Tymphi. Based on the IUCN Red List of Threatened Species (2023) *P. heldreichii*

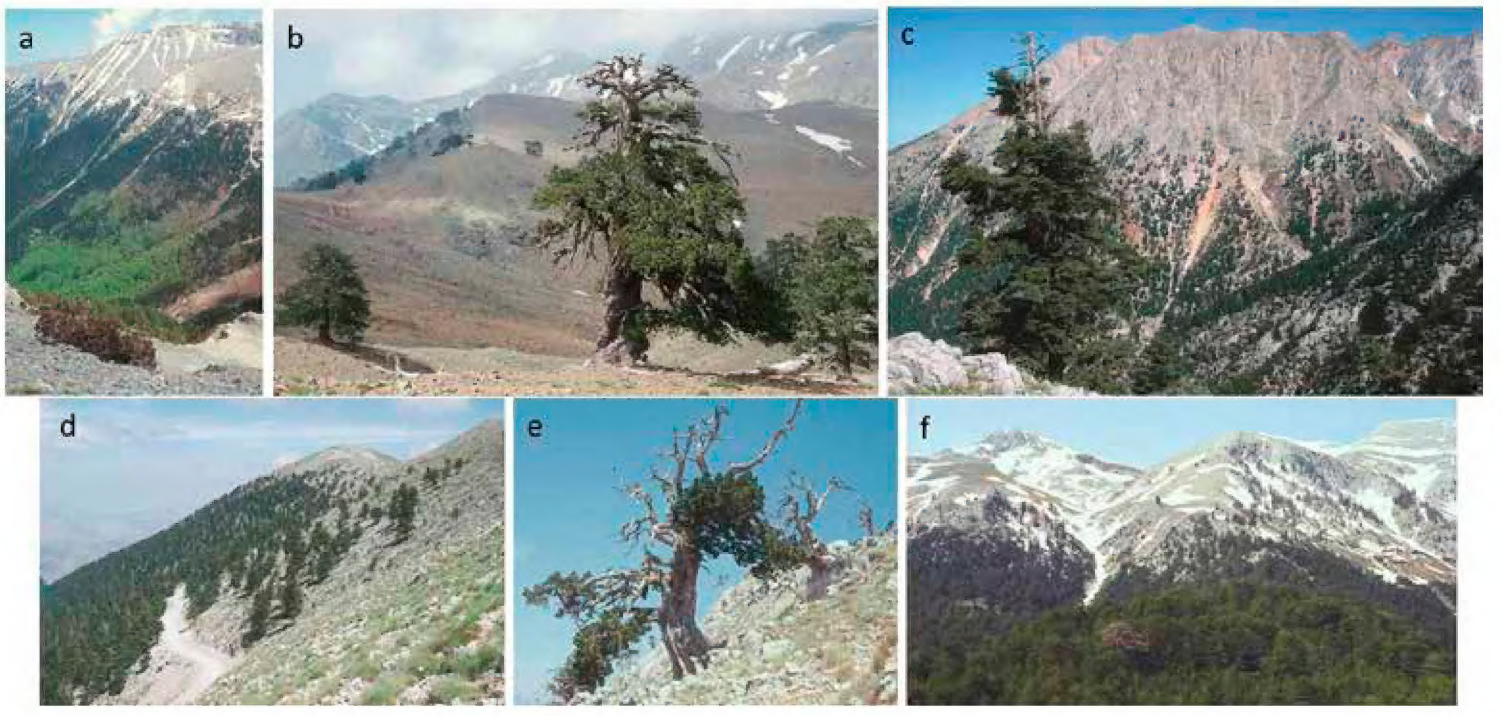

Fig. 4. Timberlines from the Greek mountains at the turn of the millennium (Brandes, 2007): (a) Mt. Olympus: View to the southern side of the Mavrolongos valley with a *Pinus heldreichii* belt above *Fagus sylvatica* stands. The forest line reaches ca. 2.100-2.200 m. Foreground: Bosnian pine "*krummholz*" at ca. 2.450 m a.s.l., (b) Mt. Smolikas: Treeline at ca. 2.150 m, formed by ancient *Pinus heldreichii*. The individual with the spike top has been dendrochronologically dated (941-2015 AD), (c) Mt. Chelmos: Orographic timberline on the southern flank of the massif, formed by *Abies cephalonica*. Treeline at ca. 1.700-1.800 m. Foreground: fir-dieback, (d) Mt. Chelmos: Highest forest line on Peloponnese (*Abies cephalonica*), reaching ca. 2.000 m altitude. Treeline and krummholz line at ca. 2.100 m, (e) Mt. Kyllini: *Juniperus foetidissima*, at ca. 1.750 m, on a SW-exposed slope. After dieback, their very decay resistant wood makes the ancient junipers develop slowly into bizarre tree ruins, (f) Mt. Taygetos: Timberline ecotone at the eastern flank of the massif, formed by *A. cephalonica* and *Pinus nigra* subsp. *nigra* (treeline at ca. 1.800-1.900 m). The tree distribution shows a clear relation to the topography and the snow cover pattern in late spring. Fir-dieback leads to a thinning of the tree stands in the ecotone (center right).

is characterized as Least Concerned-LC. Further south, the endemic *A. cephalonica* Loudon (Greek fir) -characterized also as LC (IUCN, 2023)– distributed in Central Greece and Peloponnese- and *Abies x borisii-regis* Mattf. (Bulgarian fir), a hybrid fir species native to the mountains of the Balkan Peninsula in Bulgaria, northern Greece, Kosovo, North Macedonia, Albania and Serbia, which in Greece can be found in Pindus and Central Greece, form the timberlines, on Peloponnese often together with *Pinus nigra* J.F. Arnold subsp. *nigra* (LC). *Juniperus foetidissima* Willd. (LC) occurs from the southern flanks of Mt. Tymphi to the mountains of the northern Peloponnese. But, the arboreous juniper is clearly restricted to slopes in southern exposition or more generally to the warm and dry southern and western mountain flanks. Only in a few spots *Fagus sylvatica* L. (LC) forms an abrupt forest-line in the central Pindus (Tzoumerka). On Mt. Erymanthos (NW Peloponnese) *Quercus frainetto* Ten. reaches the treeline at ca. 1.600 m a.s.l.. These last two very local and exceptional phenomena will be neglected in the following paragraphs.

Which tree species are present at the timberline depends on the climate zone and the floral history (Holtmeier, 2003). Anthropogenous influences, as well as the competition between tree species, are taking a back seat (Arno, 1984). The timberlines of Northern and Central Europe all share close floristic relations (Holtmeier, 1973), but this picture is already modified on the Balkans by the endemic species *Pinus peuce* Griseb. and *Picea omorika* (Pančić) Purk. In the high mountains of Greece tree species appear, which do not exist further north or (as in the case of *P. nigra*) do not advance to the altitudinal limit of the forests there.

After the last ice age, climate in Greece became more "Mediterranean" and caused a retreat of today' s oromediterranean conifer species into the cool and wet mountain areas (Schütt, 1994). The subsequent development of two fir species on the Hellenic peninsula is not likely to be caused by a geographical isolation of their habitats. The overlapping intersections of *Abies x borisii-regis* and *A. cephalonica* in Central Greece rather speak for an adaptation to slightly different bioclimatic conditions in the core-areas of the two species (Block, Brandes, 2001; Brandes, Ise, 2007; Papadopoulos, 2016). Just as little can the lack of *P. heldreichii* in Central and Southern Greece be explained by geographical migration barriers. In fact, the north-south running Pindus range rather forms a migration bridge for species (as many mountain ranges do; Schroeder, 1998).

Thus, the present tree species inventory in the oromediteranean forests and at the timberlines of Greece mainly mirrors the regional and local character of the Mediterranean mountain climate. Fig. 5 elucidates that an interaction of the southwards increasing summer drought and the harshness of the winter climate explains the large-scale distribution pattern of the timberline-forming tree species from the Western/Central Balkans to Crete. This fits into the picture of a meridional gradient of temperature and (summer-)precipitation shaping the alteration of the vegetation zones on the Balkans as a whole (Horvat el al., 1974; Schroeder, 1998). Regional contrasts in timberline-forming species, which are clearly related to exposition, are to be explained mainly by differences in local climate, i.e. by moisture conditions (depending mostly on the length of snow cover and on insolation; in some areas also on the positioning of mountain flanks towards the sea, with clouds bringing moisture). Already early descriptions of the Greek mountains have stressed the geo-ecological differences of northern and southern expositions (Philippson, 1948). From the high mountains of Crete Hager (1985) has provided revealing data on the strong disparities in small scale precipitation patterns (upwind vs. lee-side positions of the mountains towards the sea).

Obviously in the area around 40°N (Mt. Olympus, Mt. Smolikas, Mt. Tymphi) very particular climate-ecological conditions prevail, which secure to *P. heldreichii* an undisputed position in the plant cover of these mountains. Only Bosnian pines can withstand the very cold winters there, also surviving mild summer-droughts or even severe and prolonged drought events (Schweingruber, 1993; Scheithauer et al., 2009; Klippel et al., 2017; 2018; Esper et al., 2021; Christopoulou et al., 2022a). The advance of *P. heldreichii* into the mountain forests of the central Balkans is limited by its low competition power against other tree species (Walter, 1975). At the timberline, where

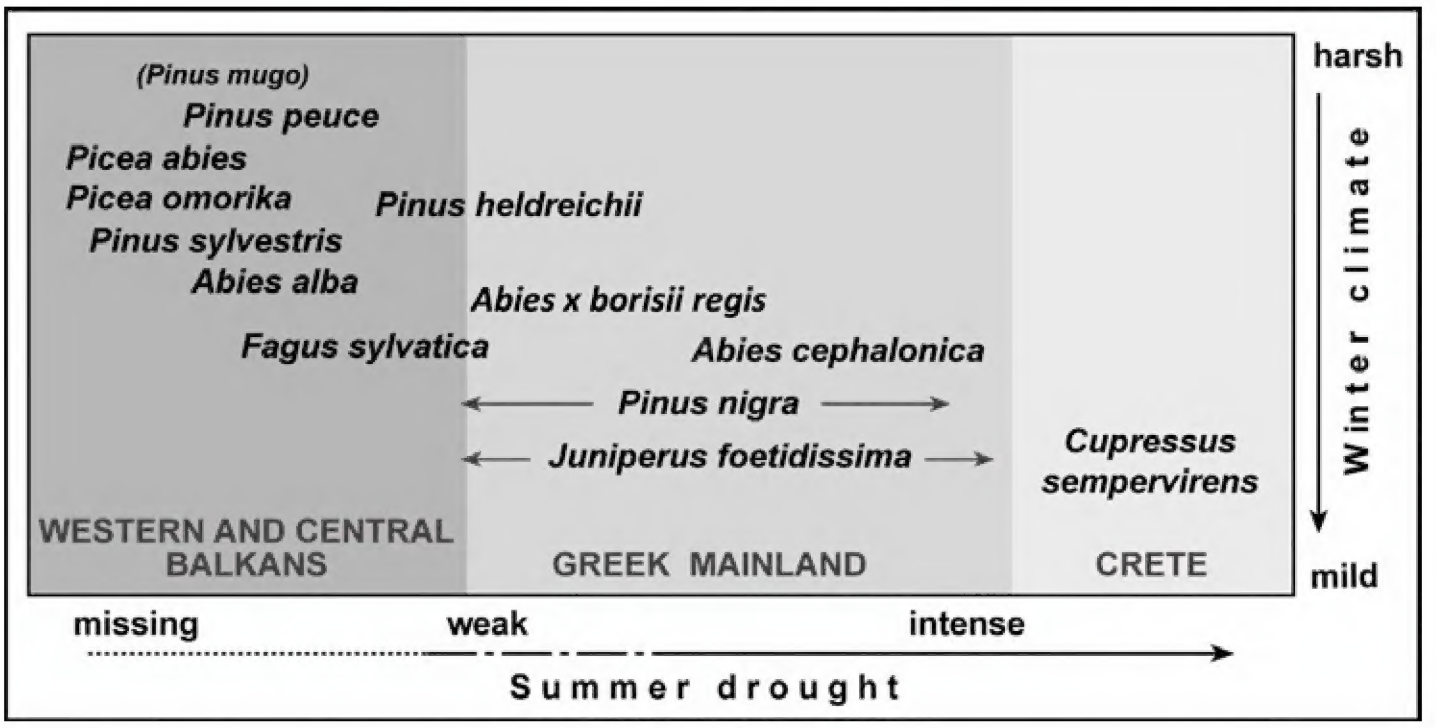

Fig. 5. Ecogram of the timberline-forming tree species in Southeastern Europe (Brandes 2007, modified)

not competition, but the autecology of the tree species plays the decisive role, the dominance of Bosnian pine is prove for a relatively cold winter climate in the three northern research areas. It explains why black pine, fir and beech are no more to be found in the pure stands of *P. heldreichii* above ca. 1.800-2.000 m a.s.l.. Interestingly, the southern distribution limit of *P. heldreichii* is set very abruptly. The sudden and total disappearance of Bosnian pine at the southern flanks of Mt. Tymphi and at the southwestern flank of Mt. Olympus (Fig. 3), gives an indication that this is related to dry climate and site conditions, which become effective there.

The presence of *Pinus nigra* at the timberlines is subject to more complex interrelations. Fire plays a paramount role for the occurrence of black pine in the oromediterranean forests. Without fire pure fir forests establish themselves (Brandes, Christopoulou, 2020). This may explain the absence of *P. nigra* at some timberlines, especially in Central Greece (no black pine stands in the mountain forests and therefore no pines advancing to the timberline). On Mt. Tymphi, Mt. Smolikas and Mt. Olympus, a thermic altitudinal limitation of *P. nigra* becomes obvious in the existence of a pure Bosnian pine belt in the upper oromediterranean zone. The fact that black pine advances at the timberlines on Peloponnese up to 1.800-2.000 m a.s.l. is an indication for relatively mild winters there. *Pinus nigra* can withstand summer drought and extreme drought periods, even on dry, rocky sites, as dendrochronogical research has proven (i.e. Schweingruber, 1993; Brandes, 2007; 2009). Only on slopes dominated by *Juniperus foetidissima,* the site conditions seem to be too dry for the existence of black pine (no mixed stands of these two species). This is ecologically plausible since too dry site conditions also explain why black pine cannot invade the mesomediterranean zone.

The stinking juniper, *J. foetidissima*, has a special position in the Greek timberlines. This cold and drought-resistant, but poorly competitive species, stays restricted to very dry sites, i.e. mainly to mountain flanks with southerly exposition or to south-

ern slopes. Arboreous juniper species typically form open forests and occur at the upper timberlines in many semi-arid and arid mountain ranges, as in Morocco, Turkey, the Himalayas and other mountains of Central Asia (Strid, 1986; Bräuning, 1999; Holtmeier, 2003).

The altitudinal limits of the two endemic *Abies* spp., which are present at the timberlines, are determined by the harshness of winter climate. This explains why fir, regardless of its shade-tolerance, cannot migrate into the Bosnian pine forests. But, three observations indicate that the presence of fir is also limited by dry conditions. First, southwards increasing summer drought causes the replacement of *Abies x borisii-regis* by *A. cephalonica*. Second, on extremely dry sites *Abies* is often replaced uphill by *J. foetidissima*, which becomes the timberline forming species above fir stands (for example on Mt. Erymanthos and Mt. Giona, Fig. 3). Third, drought stress causes the widespread phenomenon of fir-dieback in Greek forests. It occurs at different altitudes, up to the timberline, both in pure and mixed stands with juniper or black pine (Brandes, 2007; 2009; Brandes, Ise, 2007; Brandes, Christopoulou, 2020).

Timberline altitude and ecotone structure

The highest altitudes of the Greek timberlines correlate with the presence of *P. heldreichii* as timberline-forming species (Fig. 3). Especially the treeline and the tree-species line in the three northernmost areas Mt. Olympus, Mt. Smolikas and Mt. Tymphi reach much higher up (2.200-2.700 m) than in Central Greece (1.800-2.000 m) or on Peloponnese (1.800-2.100 m). Seeming paradox at first glance, the Hellenic timberlines do not rise up (continually) south-wards, since this is contradictory to the prevailing understanding of the upper timberline as "heat deficiency limit" (a complex factor, affecting tree growth in different ways, inter alia by shortness of the growing season, long-lasting snow cover, low air and soil temperatures; Holtmeier, 2003). The altitudinal limits of tree growth on the Hellenic peninsula are higher than in the Alps, which indicates milder winters in Greece. Yet, compared to other subtropical high mountains between 30° and 40°N, where timberlines can reach 3.000-4.000 m a.s.l., the altitude of the Greek timberlines is remarkably low (Körner, 1998; Holtmeier, 2003).

The Hellenic timberlines are very seldom formed by an "abrupt" forest line, but mostly show an uphill decomposition of tree stands, leading to open forests and ecotones. The vertical extent of the ecotones differs a lot, depending on whether there is an early thinning of the tree stands or even a (local) zonal differentiation into forest line, treeline, krummolz line and tree-species line (Fig. 2). In most of the research areas the tree-species line corresponds mainly to the treeline. In these cases, the presence of "*krummholz*" stays a punctual, local phenomenon, as in avalanche chutes or other places with snow movements. Only in few places locally high wind speeds ("turbo"-effects caused by topography), which occur during the growing season, lead to impressive wind-trimmed (dwarf) growth or flag shaped crowns in tall trees (Brandes 2007). On Mt. Olympus, the ecotones formed by *P. heldreichii* take an exceptional position. Where Bosnian pine forms the upper belt of the oromediterranean forest, an

altitudinal zone of stunted *P. heldreichii* individuals and a *krummholz* line are actually recognizable. The uppermost specimen mark a tree-species line at up to 2.600-2.700 m a.s.l.. Usually they are only 20-40 cm tall, mostly damaged by frost impact and obviously hardly able to survive for a long time (Brandes, 2007). Xystrakis et al. (2006) described the vegetation unit *Buxus sempervirens–Pinus heldreichii* with creeping-shrub growth form Bosnian pines that resembles the *krummholz* form of *Pinus mugo* from the area "Elikodromio" on Mt Olympus.

Timberline dynamics

Since the second half of the 20th century a regeneration of tree stands has been happening in many high mountains on the Greek mainland. But, this occurs mainly on former pasture lands and forest clearings in the lower zones of the timberline ecotones, where (micro-)climatic conditions are not too extreme and (hygric) soil conditions are relatively favorable for tree growth (Brandes, Christopoulou, 2020). Especially on smooth terrain the forest cover has become denser, which locally has caused a rise of the forest line, for example on Mt. Olympus and Mt. Zireia/Kyllini (Brandes, 2007; Zindros et al., 2020; Sidiropoulou et al., 2022). On the western flank of Mt. Olympus (NE of the village Kalyvia), even a hesitant return of *P. nigra* into the open, formerly totally treeless landscape, is taking place (Fig. 3). These processes go parallel with climatic warming trends, but they happen at relatively low altitudes. Too low temperatures have never been a really limiting factor for tree growth there. This is a strong indication that the rise of the forest line is first of all a consequence of heavily reduced pastoral land use. A trend of increased annual precipitation, as documented on Mt. Zireia for 1990-2019 by Sidiropoulos et al. (2022), gives additional support. Despite of the rising forest lines (limit of the closed forest; see definition in Fig. 3) the timberlines ecotones (zone above the forest line) do not move upwards because in the Greek high mountains no general advance of the tree-species line and the treeline into higher altitudes could be observed in recent decades. The same has been documented for Crete (Beloiu et al., 2022). This stands in contrast to what has been witnessed since the 20th century in some areas of the Alps or the Rocky mountains (Peterson, 1994; Holtmeier, 2003). But even there, the simultaneousness of climate warming and reduced grazing pressure makes it difficult to assess the primary cause of the progressive timberline dynamics (Gehrig-Fasel et al., 2007).

This is also valid for Southeastern Europe and the Mediterranean. In the Central Balkan mountains in Bulgaria, since 1970 *P. peuce* has been advancing on former pasture lands from ca. 1.760 m to 2.100 m a.s.l. (Meshinev et al., 2000). In Albania, Montenegro, Spain and Italy (Apennines) a high altitude tree densification or even a locally starting treeline-advance has been documented (Piermattei et al., 2012; Vitali et al., 2019). This recent process, synchronic at all sites for 30 years, is mainly a consequence of reduced grazing, with a still unclear role of climate. Piermattei et al. (2012) underline the complexity of timberline dynamics in the Apennines, regarding the manifold aspects of regeneration, climate, topography and human disturbance.

The disentangling of their individual roles is difficult, representing an essential challenge for timberline research in the Mediterranean.

Global warming leads to the general assumption of vegetation zones and timberlines moving upward (Spanos et al., 2021; Beloiu et al., 2022; Sidiropoulou et al., 2022). Yet, at the Greek high mountain timberlines in fact the opposite can be observed. In areas with *Abies* as timberline-forming tree species, the most striking dynamic process is fir-dieback (accompanied by insufficient or total lack of rejuvenation). Where it happens at the upper margin of the timberline ecotone, it leads here and there to a decline of the treeline altitude by 50-200 m, as on the eastern flank of Mt. Taygetos (Brandes, Christopoulou, 2020). In mixed stands of *Abies* spp. and *P. nigra* or *J. foetidissima*, the selective fir-dieback causes a thinning of the tree stands (Brandes, 2007).

Discussion – The ecology of Greek timberlines

The physiognomy and dynamics of upper timberlines are commonly caused by various intertwined factor-complexes (inter alia: topographic-, geologic/edaphic-, climatic-factors, anthropogenic impacts, dynamic biotic processes and tree species characteristics). This speaks in general against pinpointing a single factor as determining for timberline ecology. Moreover, it has to be considered that the present state of timberlines always reflects the (mostly unknown) site and climate history as well (Holtmeier, 2003). In the following paragraphs the most important timberline-forming factors in the Greek high mountains are presented.

Human influence

The Greek mountains have been subjected to human influence since ancient times. But, this does not mean that the Hellenic timberlines are purely shaped by anthropogenic force. Repeated phases of cultural declines in the long history of Greece have given long periods of recovery to the forests, too (Meiggs, 1982). Moreover, many mountain slopes are of steep, rocky terrain and remain difficult to access during all times. There, fully natural, so-called "orographic" timberlines exist.

We may assume that lumbering for building- or fire-wood did not play any paramount role at the Greek timberlines. Before the construction of forest roads in the second part of the 20th century the forests of the Greek high mountains had been very inaccessible and in most areas the transport of logs from the mountains would have been extremely difficult or impossible. Accordingly, the heavy deforestation of the 19th and early 20th century had been restricted to easily accessible areas, leaving the high mountains largely untouched (McNeill, 1992). Even in ancient times it was already more feasible to transport logs over long distances on rivers and via the sea than to move them overland (Meiggs, 1982). But this was depending on timber availability and quality. In mountainous remote areas such as the Pindus National Park wood from Bosnian pines, located close to or at the timberline, has been used for several centuries for traditional professions and crafts related to timber (logging, wood pro-

cessing, and treatment, resin collection, woodcarving, barrel making, etc.) (Christopoulou et al., 2022b). Nevertheless, still today century-old trees exist at high altitude tree-stands and at the timberlines, as dendrochronological research has revealed (Brandes, 2007; 2009; Konter et al., 2017; Christopoulou et al., 2022a), suggesting that this activity has not led to an overexploitation of the trees at the timberline.

Human influence on the high mountain vegetation without a doubt came down mainly to the practice of transhumance, i.e. the summer grazing activities with animals and herders living on the high meadows for several months (Beuermann, 1967; Sidiropoulou et al., 2022). In heavily grazed areas this did lead to a thinning of the forests, suppression of tree rejuvenation and erosion. Yet, it did not mean a total destruction of all existing trees. It has to be considered that the absolute historical peak of the grazing regime was during the high phase of (over-)population in the mountain villages, i.e. between ca. 1750 and 1950. Since the middle of the 20th century, a profound socioeconomic change has taken place in Greece, which effectuated a dramatic depopulation of the mountain villages. Parallel to this, a strong retrogression of the pasture economy took place (Thirgood, 1981; McNeill, 1992; Zindros et al. 2020). Dendrochronological research near Samarina on Mt. Smolikas and near Metsovo (two areas with heavy grazing in the above mentioned period) has shown that even then shepherds did not actively annihilate all trees in the grazing areas. Thus, the former pastoral economy has left behind very old living trees and over-aged tree stands in today' s landscape of the northern Pindus (Konter et al., 2017; Christopoulou et al., 2022a). The anthropogenic influence during this high phase of transhumance was mainly in the form of suppression of rejuvenation. Even the needs of firewood by the shepherds were limited – which becomes obvious in the existence of remarkably old deadwood (of the very decay resistant *P. heldreichii*) on Mt. Smolikas. Some has been dendrochronologically dated back to CE 575 (Klippel et al., 2017; 2018). At Mt. Taygetos we see that during the historical peak-phase of grazing, fir stands grew up; today these stands decay due to fir-dieback and also show a lack of regeneration. This is an indication of periods of favorable climatic conditions in the past. Obviously their positive influence on regeneration, growth and health of the trees at the timberline was stronger than the negative effects of the transhumant grazing regime at that time (Brandes, 2007; Brandes, Ise, 2007; Brandes, Christopoulou, 2020). In general it can be stated that the intensity of anthropogenic impact is first of all subject to a differentiation depending on topography. Only in the most easily accessible terrain of the Greek high mountains, which is suitable for grazing large flocks, a nearly total destruction of forests and trees has happened. Apart from these areas, the anthropogenic impact on the Greek timberlines is mainly to be seen in an opening of formerly denser tree stands, i.e. in a lowering of the forest line, but not in an overall lowering of the treeline or tree-species line. Bergmeier (1995) comes to a similar evaluation for the timberline (*Cupressus sempervirens*) at the southern side of the Lefka Ori, Crete.

Regarding fire and despite playing an important ecological role in the oromediterranean forests (Habeck, Reif 1994; Brandes, Christopoulou, 2020), the human influence is not a major shaping factor for the physiognomy of the timberlines.

Topography

Together with climate, topography sets the basic conditions for the shape of timberlines, since it influences the site conditions and therefore the vegetation cover (Holtmeier, 2003). The vertical extension of the Greek timberline ecotones can be high (ca. 200-600 m), but their horizontal extension is usually relatively small. This narrow width of the transition zone is typical for strong altitudinal contrasts within a small geographical area. In the high mountains of Greece, gently rising, homogeneous slopes or small high plateaus are not completely missing, but a steep rise of the terrain is the predominant characteristic of the altitudinal zones, in which the Greek timberline ecotones lie (ca. 1.600-2.600 m a.s.l.). Also the treeless peak zones mostly show a steep, cragged architecture. This topographical situation has manifold consequences on the timberline physiognomy. First of all, the advance of the closed forest is restrained, i.e. the forest line is lowered by the steep relief. Closed forests and timberlines can typically reach great altitudes and extend to their maximum climatic limits in mountain areas with evened terrain (Holtmeier, 2003). Accordingly, also the highest forest line on Peloponnese, formed by *A. cephalonica* at ca. 2.000 m a.s.l. on Mt. Chelmos, is to be found on a gently sloping mountainside (Brandes, 2007).

The interaction of steep and structured terrain with the directed climate elements "insolation" and "wind" causes a topoclimatic differentiation, leading to a small-scale change in site conditions. At high altitudes, insolation and wind strongly texture the distribution of (surface) temperatures and moisture, first of all by affecting evaporation and by relocating snow masses (accumulation in concave terrain and vice versa; Arno, 1984; Holtmeier, 2003). This becomes manifest in late spring by the distribution pattern of trees at the Greek timberlines. The highest tree stands typically grow on convex, already snow-free terrain. The concave terrain, where snow melts very late, stays treeless. All in all, the steep topography of the rather small Greek high mountain ranges seems to have a lowering effect on the timberline altitudes. Surely this is also a factor to explain why the Hellenic timberlines are at lower altitudes in comparison to other high mountains in the subtropical latitudes of the northern hemisphere (Holtmeier, 2003).

Climatic factors

Impacts of the harsh winter climate shape the physiognomy of the Greek timberline ecotones. This is most obvious in late spring by looking at the patterns of snow melt out and tree distribution at the upper margins of the timberlines: the still snow covered (concave) terrain is treeless and the already snow-free (convex) terrain carries the highest tree stands, forming the treeline. This spatiotemporal pattern of the snow cover, which is a consequence of interaction between wind, relief and insolation, reveals that trees cannot establish themselves on sites with very late snowmelt. Generally, the snow cover can have positive (e.g. protection against frost) and negative effects (e.g. short growing season) on tree growth at timberlines (Holtmeier, 2003). At the treeline and tree-species line in Greece a "right" amount of snow cover seems to be ecologically highly significant. On the one hand the snow cover has to be big enough

to provide frost protection for young trees and also moisture in the spring. On the other hand it must not be too mighty, which would cause a too late melt out. In some snow-rich places within the Greek timberline-ecotones such as avalanche chutes, trees still can establish themselves. Yet, the force of moving snow masses, occurring maybe only irregularly, e.g. in years of very abundant amounts of snow, leads to various abnormal growth forms, such as strongly curved stems, multi-stemmed growth or bayonet growth (Brandes, 2007). These are typical for cold winter treelines (Holtmeier, 2003). Especially on Mt. Olympus the avalanche chutes in the Mavrolongos valley show dense *krummholz* of *Pinus heldreichii* caused by the mechanical impact of snow movements. A combination of wind and snow cover can cause ice particle abrasion on stems, branches and needles of small, stunted "trees" at the *krummholz*-line. These are not very frequent, but exist from Mt. Olympus to Mt. Taygetos (Brandes, 2007). Ice crystals, which get driven by wind along the surface of the snow cover, mechanically damage the uphill sides of the "trees" at the upper level of the snow cover. This can lead, often in coaction with frost (drought) impact, to abnormal "flagged", "mat-", "table-" and "espalier-" like growth forms. These are to be found in an exemplary form on Mt. Olympus (Fig. 6).

Frost impact is the other winter-climate force at the Greek timberlines and corresponding damages, visible by red needles, are to be found mainly at the tree-species line, usually affecting small and stunted "trees". It is known that freezing can damage seedlings and trees in timberlines directly, typically after short periods of warm weather in winter, by sudden dehydration. In contrast, frost drought (winter desiccation) results from gradual water loss through transpiration. It mainly occurs in late winter, when needles and shoots warm up far above air temperature; the resulting steep vapour gradient between the foliage and the cold ambient air causes water loss by transpiration (Holtmeier, 2003). Frost drought is a timberline forming factor in Greece, especially on Mt. Olympus, but it does not seem to have the paramount ecological importance which some researchers have ascribed to it, for the timberlines in the high mountains outside the tropics (Tranquillini, 1979).

Fir-dieback, causing local treeline regressions, is illustrating that not only winter climate, but also drought plays an important ecological role at the Greek timberlines (Brandes, 2007; Brandes, Christopoulou, 2020). Long-term fluctuations in precipitation and severe drought periods have been revealed as typical for the Eastern Mediterranean by dendroclimatological analyses and historical records (Grove, Conterio, 1995; Xoplaki et al., 2001; Luterbacher, Xoplaki, 2003; Touchan et al., 2005). This high climatic variability has a strong influence on timberline dynamics as well (Brandes, 2007; Brandes, Christopoulou, 2020).

The "Greek timberline paradoxon" (i.e. timberline altitudes on the Hellenic peninsula not rising southwards) gives another indication that the factor complex "dryness" (a combination of seasonal lack of rainfall, high insolation and dry substrates) is an essential aspect to understand the ecology and dynamics of the Hellenic timberlines. Dryness leads to the latitudinal change in tree species and (based on their autecology) to a drop in timberline altitude. Also, the vegetation of the peaks in the

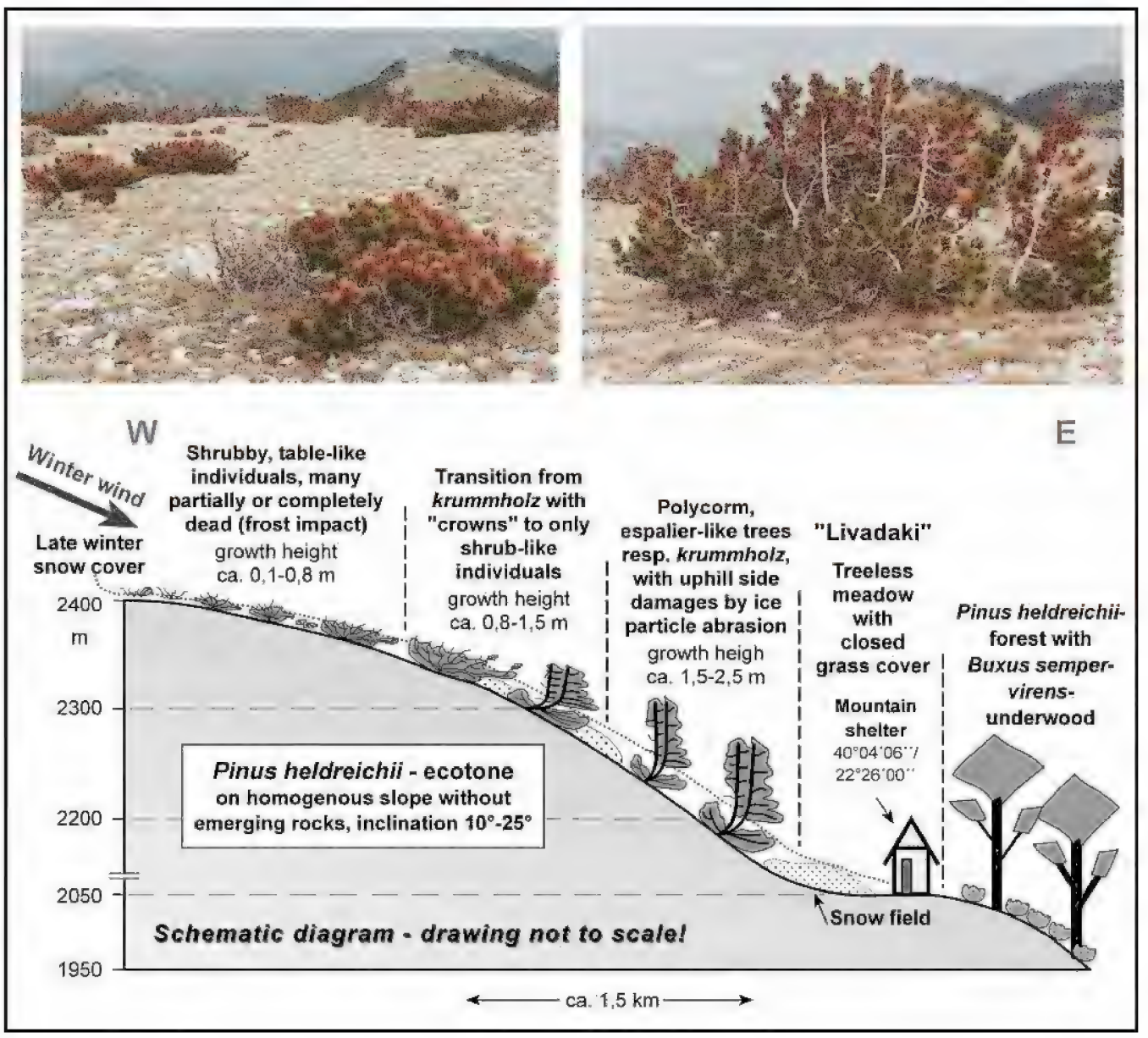
W
E
Winter wind
Late winter snow cover
Shrubby, table-like individuals, many partially or completely dead (frost impact)
growth height ca. 0,1-0,8 m
Transition from krummholz with "crowns" to only shrub-like individuals
growth height ca. 0,8-1,5 m
Polycorm, espalier-like trees resp. krummholz, with uphill side damages by ice particle abrasion
growth heigh ca. 1,5-2,5 m
"Livadaki"
Treeless meadow with closed grass cover
Mountain shelter
40°04'06'' / 22°26'00''
Pinus heldreichii-forest with Buxus sempervirens-underwood
2400 m
2300
2200
2050
1950
Pinus heldreichii - ecotone
on homogenous slope without emerging rocks, inclination 10°-25°
Schematic diagram - drawing not to scale!
Snow field
ca. 1,5 km

Fig. 6. Timberline detail at „Livadaki" / Mt. Olympus. The interaction of terrain, wind, snow cover and frost impact cause an exemplary ecotone with environmentally-induced *krummholz* (Brandes 2007, modified).

south of Greece is scantier than in the north and shows more clearly a xeromorphic character (Horvat et al, 1974).

The high ecological importance of water supply at the Greek timberlines is underlined as well by these general observations: (i) the direct vicinity of the sea, bringing moisture and cloud cover, usually lifts the regional altitude of the timberline (most prominent on Mt. Olympus); (ii) the Greek timberlines do not reach their highest position on the warm and sunny southern slopes of the mountains (as it is typically the case in the Alps or Rocky mountains; Holtmeier, 2003), but on northern and eastern mountain flanks, where snow melts late and insolation is less intense ; (iii) the process of fir-dieback is usually more severe on southern slopes than on northern expositions.

All in all the Greek timberlines must not be understood only as caused by winter climate ("heat deficiency line"), but also as shaped by the factor complex "dryness". This makes the analysis of dynamic processes, especially in relation to climate change, extremely challenging, since precipitation trends might be ecologically more relevant than an increase in air temperatures.

Biotic factors

Biotic processes are to be considered in Greek timberline ecology and contribute to the site history. This becomes visible in the wide-spread phenomenon of fir-dieback, which is a complex process framework. Drought plays the key role making stressed trees prone to attacks by bark beetles, pathogenic fungi and mistletoes. Eventually the firs die, even at high altitudes, which can lead to a local decline of the treeline (Brofas, Economidou, 1992; Markalas, 1992; Brandes, 2007; 2009; Brandes, Christopoulou, 2020). Fir-dieback and episodic bark beetle calamities seem to be fully natural phenomena, related to the severe drought events, which are an integral part of Greek climate variability. They have been documented by the Greek forest authorities since 1929 (Kailidis, Markalas, 1988).

The more drought resistant *Pinus nigra* is not affected by bark beetles and hardly by pathogenic fungi, but it can be damaged by caterpillars of the processionary moth, *Thaumetopoea pityocampa* Denis & Schiffermüller, 1775 (Lepidoptera: Notodontidae), which is an important pest in Greek pine forests. In mature forests, the attacks lead to significant losses in volume and radial growth , but usually they do not kill the trees (Kanat et al., 2005). Stunted specimen of black pine at the tree-species line of Mt. Taygetos, which were damaged by frost impact as well, showed a partial dieback of some branches after the caterpillar attack. This means that the insect damage can even contribute to irregular growth forms in the timberline ecotone (Brandes, 2007).

"Regeneration" – the key aspect to understanding the Greek timberline ecology?

In a global perspective the upper timberline is a very polymorphic phenomenon. This did lead to various theories about the reasons of its existence and to several terms related to the causality and position of timberlines (Holtmeier, 2003). In the Greek high mountains "orographic timberlines" are abundant, i.e. steep rock faces, scree or avalanche chutes decompose the forest and set an upper limit to the altitudinal advance of tree-stands. Without doubt dry substrates, thin-layered or rocky soils, contribute to the thinning of the forests at the Hellenic timberlines. Yet, they are no real "edaphic timberlines", since the adverse edaphic situation becomes effective mostly in combination with climatic drought. In many parts of the research areas the term "anthropogenic timberline" is applicable. The dry meadows are often the result of human activities and disturbances (Athanasiadis et al., 2001; Papanastasis, 2002). Nevertheless, only in a few places a total depression of the treeline and of the tree-species line has occurred. This means that also in most areas influenced by grazing the natural timberline-forming factors are neither hidden nor suspended. Thus, in all not intensely human-shaped sections of the Greek timberlines we may speak about a "climatic timberline" in the broadest sense. Yet, the term "climatic timberline" is closely connected with the understanding of the upper timberline as a "heat deficiency line" (Holtmeier, 2003). Of course at the Greek timberlines the typical altitudinal temperature decrease plays an ecological role. However, a generally too short vegetation period or too low

temperatures during the vegetation period do not seem to be effective there. In the Mediterranean Greek high mountains the term "heat deficiency" rather stands for a complex of factors, which can be effective in direct and indirect ways. In Greece it becomes manifest mainly in the form of late snow melt (concave terrain), ice-blast, freezing and frost drought. Since the term "climatic timberline" fades out the ecological role of the factor complex "dryness", it seems more adequate to speak in Greece about "climate-ecological timberlines" (Brandes, 2007).

The discussion, which mechanisms determine the transition zone between forests and the treeless zone beyond in a global perspective, brought forth various, partly interrelated hypotheses (Slatyer, Noble, 1992; Körner, 1998). These are based mainly on observations from high mountains in temperate regions (Alps, Rocky Mountains) and are categorized by Körner (1998) into "stress-, disturbance-, reproduction-, carbon balance- and growth limitation-hypothesis". The observations from Greece render it unlikely that carbon balance or growth limitation, both related to low (mean) temperatures, become generally effective there. Compared to other high mountains of the northern hemisphere, the Greek mountains are characterized by a relatively mild climate (Brandes, 2007). Moreover, the timberline altitudes in Greece are relatively low compared to other mountain areas of similar latitude. This means that primarily the "stress-, disturbance- and reproduction-hypotheses" come into effect. The fundamental aspects of the "stress-hypothesis" of Körner (1998), frost impact and desiccation (frost-drought) do not play a highly important role as at other non-tropical timberlines. Single scrub-like "trees" or seedlings, which show frost-related damages (visible by red or lost needles in springtime), can be found at the tree-species line in most of the research areas. Yet, only on Mt. Olympus, where the tree-species line reaches by far highest in Greece, this phenomenon is common and obviously an important factor for the formation of the *krummholz*- and tree-species line. It explains why *P. heldreichii* specimens, which still can establish themselves at altitudes of 2.200-2.700 m a.s.l., cannot grow into tall and upright trees anymore. Moreover, drought is part of environmental stress too and co-determines the structure and altitude of the Greek timberlines. The mentioned process of fir-dieback reveals that drought-impact should be included into the "stress-hypothesis", since it also affects tree stands in timberlines and can even lead to a local treeline decline. The "disturbance hypothesis", i.e. mechanical damage by wind, ice particle abrasion, snow-break or avalanches has to be considered as well. Yet, it is mainly a modulating aspect, causing irregular, abnormal growth forms of the forest tree species within the existing ecotones, but it is not really setting a general zonal upper limit to tree growth.

Eventually, the hypothesis related to problems of "reproduction", i.e. seed development, seed dispersal, germination and seedling establishment, seems to be of paramount importance to explain the physiognomy and altitude of the Greek timberlines. Stunted tree specimens in timberlines generally mirror a "fight for survival" of these individuals against the harsh environmental conditions and site factors. Körner (1998) mentions observations from high mountains, where trees are continually invading higher ground and are regularly being killed off. But, this is not the case

in Greece. Where trees can establish themselves at the Hellenic timberlines, the site conditions usually allow them to grow upright and more or less normal. Apart from the eastern and northern flanks of Mt. Olympus, there is no general altitudinal belt of "*krummholz*" at the Hellenic timberlines. All this leads to the conclusion that the establishment of trees, i.e. the germination of seeds and the survival of seedlings is the key aspect to understanding the Greek timberline ecology. In general the topic of generative rejuvenation in timberlines, which can be compared to a "hurdle race", is highly important. Tree seedlings are very sensitive and need a continuous series of years without any extreme hygrothermic conditions, to develop a deep root system and become resilient enough to survive (Holtmeier, 1995; Höllermann, 1978). Yet, in the Greek timberlines high-contrast (micro-)climatic conditions are not the exception but the norm. Several observations support the "regeneration hypothesis". The change of timberline-forming tree species, which cannot be explained by migration barriers, reveals that their autecology plays an important role, starting with regeneration as the fundamental topic. Since all of the timberline-forming tree species in Greece stand at the southern limits of their distribution area, it seems ecologically plausible that they are sensitive to impacts by water deficits or heat damages (drought, high insolation). Accordingly, treeline and tree-species lines reach highest in Greece on the wet, also during summer, often cloudy northern and eastern flanks of Mt. Olympus. There it is obviously moist enough so that *P. heldreichii* can germinate and seedlings can establish themselves. Yet, above ca. 2.200-2.300 m a.s.l. Bosnian pine has to fight against the environmental conditions of winter (frost impact etc.) and gets deformed to "*krummholz*".

Abies is the most widely distributed tree genus in the timberlines in central and southern Greece. But, the Greek fir is per se a shade-tolerant species and generally does not regenerate well on open sunny sites and on dry soils (Politi et al., 2009; Christopoulou et al., 2018), as they prevail at the timberlines. This is why in the oromediterranean forests of southern Greece usually *P. nigra*, a typical pioneer species, starts the forest recovery on open sites, initiating a mosaic cycle (Brandes, Christopoulou, 2020). Studies about the regeneration of oromediterranean forests after wildfires have yielded interesting results, which also have meaning for the timberline ecotones and support the regeneration hypothesis. In fir- as well as in black pine-forests, regeneration strongly depends on the distance to older trees, providing seeds. *Abies* spp. and *P. nigra* both have anemochorous seed dispersal, which makes (uphill) seed dispersal in the timberline ecotones as such difficult, and generally limits the quantity of available seeds there. Moreover, the studies on oromediterranean forest regeneration have revealed that dry site conditions endanger the survival of seedlings (be they planted or of natural settling) and that regeneration success depends mainly on favorable microhabitats. Where seedlings and saplings are better protected (for example by coarse woody debris) from high temperatures and excessive water loss, regeneration density is higher (Christopoulou et al., 2014; 2018; Raftoyannis, Spanos, 2015). Another parallel between the timberline ecotones and burned sites is the fact that regeneration often happens most successfully in the shade of older trees (Brandes, 2007; Politi et

al., 2009). Often the uppermost trees and tree stands at the Greek timberlines grow on "protected" microsites, as they exist e.g. under favor of bigger rocks. Moreover, it can frequently be observed that young trees grow out of low *J. communis* bushes, where they obviously took profit from balanced micro-climatic and hygric conditions, which favored their germination and growth.

At the upper margins of the Greek timberline, the ecotone terrain with very late snow melt stays treeless. This can be explained because these sites are too wet and cool for the establishment of trees. Also, these are the only places in the Hellenic high mountains, where dense, closed grasses cover exists making it difficult for tree seeds to germinate due to competition. The occurrence of strong frost impact on the ground and in the top layer of the soil comes to the fore in the form of periglacial phenomena, such as frost weathering, solifluction and needle ice. Their occurrence is favored by the low degree of vegetation cover and the widespread open soils with fine earth. According to Hagedorn (1969) the lower limits of solifluction in the Greek high mountains lie at 1.950-2.300 m a.s.l.. Brandes (2007) first observed needle ice at only 1.450 m a.s.l. on Mt. Taygetos, in April 1996. This means: where tree seedlings are not protected by the "right" amount of snow cover and the substrate is exposed to frequent frost change, they can easily be deadened, either by direct freezing of the plants or by mechanical, frost-dynamic processes, which destroy the fine roots of seedlings or push them out of the soil (Holtmeier, 2003).

During summer, high insolation can not only lead to a drying-out of the substrate, but also to a lethal overheating of soil surfaces. Solar radiation increases exponentially with altitude, due to the lower concentration of vapor in the higher atmosphere (Holtmeier, 2003). The Mediterranean mountain climate of Greece, with many cloudless days, makes it very likely that this is an important aspect there. The microclimatic measurements of Hager (1985) in the thorn-cushion plant formations of Crete have proven maximum soil surface temperatures of 50-70 °C. Top soil temperatures of only 40-50 °C can already cause fatal physiological damages on roots and shoots of seedlings and even young trees (Tranquillini, 1979; Höllermann, 1978; Holtmeier, 2003). This explains the high mortality rate of seedlings recorded for several tree species during the first summer period (e.g. Thanos et al., 1989; Ordóñez, Retana, 2004; Politi et al., 2009).

It has been shown that competition with the low vegetation plays an important, restraining role for the establishment of trees at many timberlines, as in the Alps (Körner, 1998). Yet, in Greece this is generally not the case – which speaks again for the ecological importance of microclimatic extremes. The vegetation above the timberline is mostly formed by half-open dry meadows. Their degree of cover is typically between 30-80 % (Quézel, 1964), in Peloponnese often only 20-50 % (Strid, Tan, 1996). These plant formations are characterized by high species diversity and endemism, both of which increase from north to south (Quézel, 1964; 1967; Dimopoulos, Georgiadis, 1992). One reason for this is the low competition at the open sites near and above the timberline (Horvat et al., 1974). A close look at the physiognomy of the dominant taxa is probably most suitable to support the hypothesis that harsh microclimatic condi-

tions strongly impede the successful establishment of trees above the current timberline ecotones. The xeromorphic features of many taxa are mainly adaptations against harmful ultraviolet radiation, overheating of surfaces and water loss by transpiration. In addition, supporting sclerenchyma tissues and leaf hairiness are beneficial against the impact of dryness and frost drought (Richter, 1996). Owing to their physiognomy the xerophytic plant formations are also called "thorn cushion meadows" or "prickly thrifts", because apart from the tussock grasses hemispherical, densely ramified and often spiny dwarf scrubs, such as *Astragalus* spp., are their characteristic elements (Horvat et al., 1974; Barbéro et al., 1975). Such thorn cushion formations are typical constituents of the mountain vegetation in winter-rain areas, between 35° and 40°N. The growth form of the hemispherical bushes is an adaptation to special environmental conditions. Since the plants are exposed to an extreme microclimate, which in regard to temperature and air moisture differs a lot from the macroclimate, the air held inside the cushion shall act as buffer against vapor pressure deficits and extreme temperature fluctuations (Hager, 1985; Richter, 1996). Indeed Hager (1985) measured on Crete 20-30°C lower temperatures inside the cushion plants than at the surrounding soil surfaces. Thus, these oreophytes mirror the extreme climate-ecological conditions in the Greek high mountains. Their adaptations are evidence that even at high altitudes the Mediterranean climate rhythm, intensified by arid substrates, has a profound influence on plant life.

Climate change and future timberline dynamics in Greece

Vegetation and timberline dynamics related to climate change stand in a global scientific focus and rightly deserve attention. In Greece, the oromediterranean forests would clearly be endangered by a warmer and drier climate, which would lead to a narrowing of their habitat (Brandes, Christopoulou, 2020; Spanos et al., 2021). The present results about the timberline ecology show that influences of winter and summer climate, both causing extreme site conditions, especially for seedlings and young trees, play a role. Hence, only a scenario of milder winters in combination with higher rainfall during the vegetation period could lead to a broad ascent of the Greek timberlines. Results from Crete confirm that an increase of the mean annual temperature over the last 70 years, which was going along with a decrease of precipitation, did not cause a treeline shift (Beloiu et al., 2022).

Several climate studies predict for the 21st century a warming trend over Greece, associated with a decrease in summer precipitation and an increase in summer temperatures as well as in the frequency of drought events and heat waves (Gao, Giorgi, 2008; Giorgi, Lionello, 2008; Fischer, Schar, 2010; Nastos, Kapsomenakis, 2015), as it is already recorded from 2021 (Founda et al., 2022) till 2023. This trend would rather cause regressive timberline dynamics, at least where *Abies* is the timberline forming species (disintegration of tree stands or decline of the treeline by fir-dieback). However, with *P. nigra* and *J. foetidissima* also highly drought-resistant species form the Hellenic timberlines, and not only in the area of *P. heldreichii* aspects of the regional

climate need to be considered (e.g. by the proximity of the sea, as on Mt. Olympus). Therefore, on the whole an estimation of the future timberline dynamics remains very difficult (Brandes, 2007). Not only in Greece this question demands a differentiation in spatial as well as in floristic regards (autecology of the tree species) and it requires a complex landscape-ecological approach (Holtmeier, 2003).

The discovery of obviously ancient Bosnian pines at the timberline of Mt. Smolikas by Brandes (2007) has already spurred intensive dendrochronological studies on *P. heldreichii* there (Konter et al., 2017; Klippel et al., 2017; 2018; Esper et al., 2021). Remote places at the Greek timberlines still harbor very old trees (ages between 500-1.000 years) and deadwood. Trees at timberlines are a valuable geoarchive, which provides interesting insights into the climate-history and climate-ecology of Southeastern Europe (Scheithauer et al., 2009). Against the background of climate change, dendrochronological research enables us to put climatic trends or extremes into perspective and to develop a picture of what is "normal" (Schweingruber, 1988). Dendroecological research also helps to understand the climate-growth relations of tree-life at the timberline. But, it has to be considered that it can provide only limited explanations about timberline ecology and dynamics. Regeneration mechanisms, especially the multifold spatio-temporal "hurdles" of successful seedling establishment (seed dispersal, short-term microclimatic extremes etc.), cannot be covered by tree-ring analyses.

Conclusions and suggestions for further research

The present review article has provided fundamental information about the tree species, physiognomy and dynamics of the high-mountain timberlines on the Greek mainland. An ecological interpretation has revealed that they are shaped by a complex of human, abiotic and biotic factors. "Regeneration" seems to be a key issue. The strong seasonal contrast between summer and winter conditions, both causing harsh microclimatic extremes, has a paramount climate-ecological significance.

Many questions remain open, especially regarding recent and potential future timberline transformations. In general, analyses of vegetation dynamics at the timberlines of the Mediterranean face first of all the challenge to identify the main driving forces. Effects of changes in land use such as the stop or reduction of grazing in recent decades and climatic effects of global warming overlap each other in a complex way. This makes an assessment and disentanglement of the individual timberline-forming factors highly difficult.

For a better geo-ecological understanding of the Greek timberlines macro- and microclimatic research as well as detailed studies on aspects of tree regeneration and seedling establishment at high altitudes would be desirable. Timberline analyses based mainly on mean climatic data, not considering periodic extreme climatic events or micro-climatic conditions, will not prove very helpful to understand timberline dynamics in relation to a changing climate.

A survey by commercially available drones would be a feasible and cheap way to perform timberline-monitoring as a basis for any further analysis. Particularly interesting spots with recognizable dynamics should be identified as permanent observation plots clearly defined by scientifically published GPS data. Documentation from the air and on the ground, being carried out in time intervals of five years, would provide a sound scientific assessment of the vegetation dynamics at the Hellenic timberlines. The mountains cover a huge part of the country, host unique flora and fauna and offer multiple ecosystem services (Kokkoris et al., 2018). Therefore, they should be properly studied and protected, especially under the risk of climate change.

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References

Aakala T., Hari P., Dengel S., Newberry S.L., Mizunuma T., Grace J. 2014. A prominent stepwise advance of the tree line in north-east Finland. Journal of Ecology 102(6), 1582-1591. https://doi.org/10.1111/1365-2745.12308

Armand A.D. 1992. Sharp and gradual mountain timberline as a result of species inter-actions. In: Hansen A.J., Di Castri F. (Eds.) Landscape boundaries. Consequences for Biotic Diversity and Ecological Flows. (=Ecological studies, Vol. 92). New York, USA, 360-378.

Arno S.F. 1984. Timberline: mountain and arctic forest frontiers. Seattle, 304 pp.

Athanasiadis N. 1974. Zur postglazialen Vegetationsentwicklung von Litochoro Katerinis und Pertouli Trikalon (Griechenland). Dissertation, Universität Basel.

Athanasiadis N., Eleutheriadou E., Theodoropoulos K. 2001. Flora and Vegetation of Greece; Publications Department of Aristotle University of Thessaloniki: Thessaloniki, Greece, p. 76. (in Greek).

Barbéro M., Bonin G., Quézel P. 1975. Les pelouses écorchées des montagnes Circum-Méditerranèennes. Phytocoenologia 1(4), 427-459.

Beloiu M., Poursanidis D., Tsakirakis A., Chrysoulakis N., Hoffmann S., Lymberakis P., Barnias A., Kienle D., Beierkuhnlein C. 2022. No treeline shift despite climate change over the last 70 years. Forest Ecosystems 9, 100002. https://doi.org/10.1016/j.fecs.2022.100002

Bergmeier E. 1995. Die Höhenstufung der Vegetation in Südwest-Kreta (Griechenland) entlang eines 2450 m – Transsektes. Phytocoenologia 25(3), 317-361.

Beuermann A. 1967. Fernweidewirtschaft in Südosteuropa. Braunschweig, 232 pp.

Block M., Brandes R. 2001. Dynamik und Strukturwandel mediterraner Tannenwälder in Südspanien und Südgriechenland. – Mitt.d. Fränkischen Geographischen Gesellschaft 48, 305-335.

Bolle H.-J. (Ed.) 2003. Mediterranean Climate. Variability and Trends. Springer, Heidelberg, Berlin, Germany, 371 pp. https://doi.org/10.1007/978-3-642-55657-9

Bräuning A. 1999. Zur Dendroklimatologie Hochtibets während des letzten Jahrtausends. Stuttgart. Dissertationes Botanicae, 312.

Brandes R. 2007. Waldgrenzen griechischer Hochgebirge. Unter besonderer Berücksichtigung des Taygetos, Südpeloponnes (Walddynamik, Tannensterben, Dendrochronologie). Dissertation University Erlangen-Nuernberg, Germany – Erlanger Geographische Arbeiten, Sonderband 36, 296 pp. http://nbn-resolving.de/urn:nbn:de:bvb:29-opus-5410

Brandes R., Ise M. 2007. Fingerprints of climate change in Mediterranean mountain forests? – Observations on Mediterranean fir species threatened by climate change. Geo-Öko 28, 1-26.

Brandes R. 2009. Dendrochronology on *Pinus nigra* in the Taygetos mountains, southern Peloponnisos. In: Manning SW, Bruce M.J. (Eds.). Tree-rings, Kings, and Old World Archaeology and Environment (Papers presented in honor of Peter Ian Kuniholm). Oxford, UK, 81-95.

Brandes R., Christopoulou A. 2020. Long-term forest dynamics of oromediterranean fir forests in Greece. South-east European forestry 11(1), 71-84. https://doi.org/10.15177/seefor.20-02

Brofas G., Economidou E. 1994. Le dépérissement du Sapin du Mont Parnasse (Grèce). Le rôle des conditions climatiques et écologiques. Ecologia Mediterranea 20(1/2), 1-8.

Christopoulou A., Fyllas N., Andriopoulos P., Koutsias N., Dimitrakopoulos P., Arianoutsou M. 2014. Post-fire regeneration patterns of *Pinus nigra* in a recently burned area in Mount Taygetos, Southern Greece: the role of unburned forest patches. Forest Ecology and Management 327, 148-156. https://doi.org/10.1016/j.foreco.2014.05.006

Christopoulou A., Kazanis D., Fyllas N.M., Arianoutsou M. 2018. Post-fire recovery of *Abies cephalonica* forest communities: the case of Parnitha National Park, Attica, Greece. iForest 11, 757-764. https://doi.org/10.3832/ifor2744-011

Christopoulou A., Fyllas N., Gminska-Novak B., Özarslan Y., Arianoutsou M., Brandes R., Wazny T. 2022a. Exploring the past of Mavrovouni forest in the Pindus Mountain range (Greece) using tree rings of Bosnian pines. Trees 36, 153-166. https://doi.org/10.1007/s00468-021-02189-6

Christopoulou A., Gmińska-Nowak B., Tsakanika E., Ważny T. 2022b. Discovering the unknown history of the utilization of *Pinus heldreichii* in wooden structures by means of dendroarchaeology: a case study from Metsovo (Northern Greece). Forests 13, 719. https://doi.org/10.3390/f13050719

Delcourt P.A., Delcourt H.R. 1992. Ecotone Dynamics in Space and Time. In: Hansen A.J., Di Castri F. (Eds.). Landscape boundaries – Consequences for Biotic Diversity and Ecological Flows. (=Ecological studies, Vol. 92). New York, USA, 19-54.

Dimopoulos P., Georgiadis T. 1992. Floristic and phytogeographical analysis of Mount Killini (NE Peloponnisos, Greece). Phyton 32(2), 283-305.

Elliott-Fisk D.L. 2000. The Taiga and boreal forest. In: Barbour M.G., Billings M.D. (Eds.). North American Terrestrial Vegetation. Cambridge University Press, New York, 41-73.

Esper J., Konter O., Klippel L., Krusic P.J., Büntgen U. 2021. Pre-instrumental summer precipitation variability in northwestern Greece from a high-elevation *Pinus heldreichii* network – International Journal of Climatology 41, 2828–2839.

Fischer E.M., Schar C. 2010. Consistent geographical patterns of changes in high-impact European heatwaves. Nature Geoscience 3, 398-403. https://doi.org/10.1038/ngeo866

Founda D., Katavoutas G., Pierros F., Mihalopoulos N. 2022. The extreme heat wave of 2021 in Greece: intensity, duration, cumulative heat and all-time records on centennial scale. EGU General Assembly Vienna, Austria, 23–27 May 2022, EGU22-5319, https://doi.org/10.5194/egusphere-egu22-5319, 2022.

Gao X.J., Giorgi F. 2008. Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. Global Planet Change 62(3-4), 195-209. https://doi.org/10.1016/jgloplacha.2008.02.002

Gehrig-Fasel J., Guisan A., Zimmermann N. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? Journal of Vegetation Science 18, 571-582.

Giorgi F., Lionello P..2008. Climate change projections for the Mediterranean region. Global Planet Change 63(2-3), 90-104. https://doi.org/10.1016/j.gloplacha.2007.09.005.

Grove J.M., Conterio A. 1995. The climate of Crete in the sixteenth and seventeenth centuries. Climatic Change 30, 223-247.

Habeck F., Reif A. 1994. Die Waldgesellschaften der montanen und subalpinen Stufe des Ostabfalls des Olymp, Griechenland. Phytocoenologia 22(4), 501-536.

Hagedorn J. 1969. Beiträge zur Quartärmorphologie griechischer Hochgebirge. Habilitationsschrift, Universität Göttingen. = Göttinger Geogr. Abh., 50.

Hager J. 1985. Pflanzenökologische Untersuchungen in den subalpinen Dornpolsterfluren Kretas. Vaduz. Dissertationes Botanicae, 89.

Hansen A.J., Risser P.G., Di Castri F. 1992. Biodiversity and ecological flows across ecotones. – In: Hansen A.J., Di Castri F. (Eds.). Landscape boundaries – Consequences for Biotic Diversity and Ecological Flows. (=Ecological studies, Vol. 92). New York, USA, 423-438.

Heikkinen O., Obrebska-Starkel B., Tuhkanen S. 1995. Introduction: the timberline – a changing battlefront. Zeszty Naukowe Uniwersytetu Jagiellonskiego 1156. Prace Geograficzne – Zeszy 98, 7 – 16.

Höllermann P.W. 1978. Geoecological aspects of the upper timberline in Tenerife, Canary Islands. Arctic and Alpine Research 10(2), 365-382.

Holtmeier F.K. 1973. Geoecological aspects of timberlines in Northern and Central Europe. Arctic and Alpine Research 5(3, Pt. 2), A45-A54.

Holtmeier F.K. 1995. Waldgrenzen und Klimaschwankungen. Ökologische Aspekte eines vieldiskutierten Phänomens. Geoökodynamik 16, 1-24.

Holtmeier F.K. 2003. Mountain Timberlines. Ecology, Patchiness and Dynamics (Advances in Global Change Research). Dordrecht, The Netherlands. 438 pp., https://doi.org/10.1007/978-1-4020-9705-8

Horvat I., Glavač V., Ellenberg H. 1974. Vegetation Südosteuropas. Fischer, Stuttgart, 768 pp.

IUCN. 2023. The IUCN Red List of Threatened Species. Version 2023-1. https://www.iucnredlist.org. Accessed on 15 January 2023.

Jørgensen S.E. 2009. Ecosystem Ecology. Academic Press, London. 521 pp.

Kailidis D., Markalas S. 1988. Dürreperioden in Zusammenhang mit sekundärem Absterben und Massenvermehrungen rindenbrütender Insekten in den Wäldern Griechenlands. Anz. Schädlingskunde, Pflanzenschutz, Umweltschutz 61, 25-30.

Kanat M., Alma M.H., Sivrikaya F. 2005. Effect of defoliation by *Thaumetopoea pityocampa* (Den. & Schiff.) (Lepidoptera: Thaumetopoeidae) on annual diameter increment of *Pinus brutia* Ten. in Turkey. Annals of Forest Science 62(1), 91-94. 10.1051/forest:2004095

Klippel L., Krusic P.J., Brandes R., Hartl-Meier C., Trouet V., Meko M., Esper J. 2017. High-elevation inter-site differences in Mount Smolikas tree-ring width data. Dendrochronologia 44, 164-173. https://dx.doi.org/10.1016/j.dendro.2017.05.006

Klippel L., Krusic P.J., Brandes R., Hartl C., Belmecheri S., Dienst M., Esper J. 2018. A 1286-year hydro-climate reconstruction for the Balkan Peninsula. Boreas 47(4), 1218-1229. https://doi.org/10.1111/bor.12320

Kokkoris I.P., Drakou E.G., Maes J., Dimopoulos P. 2018. Ecosystem services supply in protected mountains of Greece: setting the baseline for conservation management. Interna-

tional Journal of Biodiversity Science, Ecosystem Services & Management 14(1), 45-59. 10.1080/21513732.2017.1415974

Konter O., Krusic P.J., Trouet V., Esper J. 2017. Meet Adonis, Europe´s oldest dendrochronologically dated tree. Dendrochronologia 42, 12. http://dx.doi.org/ 10.1016/j.dendro.2016.12.001

Körner Ch. 1998. A re-assessment of high-elevation treeline positions and their explanation. Oecologia 115, 445-459.

Körner C. 2012. Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits. Springer Basel, pp. XI, 220. https://doi.org/10.1007/978-3-0348-0396-0

Luterbacher J., Xoplaki E. 2003. 500-year winter temperature and precipitation variability over the Mediterranean area and its connection to the large-scale atmospheric circulation. In: Bolle H.-J. (Ed.). Mediterranean Climate. Variability and Trends. Springer, Heidelberg, Berlin, Germany, 133-153.

Markalas S. 1992. Site and stand factors related to mortality rate in a fir forest after combined incidence of drought and insect attack. Forest Ecology and Management 47, 367-374.

McNeill J.R. 1992. The mountains of the Mediterranean world: an environmental history. New York, Cambridge University Press, 423 pp.

Meiggs R. 1982. Trees and timber in the ancient Mediterranean world. Oxford, Clarendron Press, xviii+553 pp.

Meshinev T., Apostolova I., Koleva E. 2000. Influence of warming on timberline rising: a case study on *Pinus peuce* Griseb. in Bulgaria. Phytoceonologia 30(3-4), 431-438.

Nastos P.T., Kapsomenakis J. 2015. Regional climate models simulations of extreme air temperature in Greece. Abnormal or common records in the future climate? Atmospheric Research 152, 43-60. https://doi.org/10.1016/j.atmosres.2014.02.005.

Ordóñez J.L., Retana J. 2004. Early reduction of post-fire recruitment of Pinus nigra by post-dispersal seed predation in different time-since-fire habitats. Ecography 27, 449–458.

Pauli H., Gottfried M., Grabherr G. 2001. High summits of the Alps in a changing climate. In: Walther G.-R., Burga C.A., Edwards P.J. (Eds.). "Fingerprints" of Climate Change. Adapted behaviour and shifting species ranges. Springer New York, New York, 139-150.

Papadopoulos A. 2016. Tree ring patterns and climate response of Mediterranean fir populations in Central Greece. Dendrochronologia 40, 17-25.

Papanastasis V. 2002. Ecology and management of pseudoalpine rangelands. In: Proceedings of the Rangeland Management and Development of Mountainous Areas, Karpenisi, Greece, 4–6 September, 437–445. (in Greek).

Peterson D.L. 1994. Recent changes in the growth and establishment of subalpine conifers in Western North America. In: Beniston M. (Ed.). Mountain environments in changing climates, London, 234-243.

Philippson A. 1948. Das Klima Griechenlands. Bonn, 238 pp.

Piermattei A., Renzaglia F., Urbinati C. 2012. Recent expansion of *Pinus nigra* Arn. above the timberline in the central Apennines, Italy. Annals of Forest Science 69, 509-517. 10.1007/s13595-012-0207-2

Politi P.I., Arianoutsou M., Stamou G.P. 2009. Patterns of *Abies cephalonica* seedling recruitment in Mount Aenos National Park, Cephalonia, Greece. Forest Ecology and Management 258, 1120-1136. https://doi.org/10.1016/j.foreco.2009.05.038.

POWO 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/ Retrieved 15 January 2024.

Quézel P. 1964. Végétation des hautes montagnes de la Grèce méridionale. Vegetatio 12(5-6), 289-385.
Quézel P. 1967. La végétation des hautes sommets du Pinde et de l`Olympe de Thessalie. Vegetatio 14, 127-228.
Raftoyannis Y., Spanos I. 2015. Regeneration of *Abies cephalonica* Loudon after a large fire in Central Greece. South-east European forestry 6(1), 1-10. https://doi.org/10.15177/seefor.15-04.
Rathjens C. 1982. Geographie des Hochgebirges. Teil 1: Der Naturraum. Stuttgart, 216 pp.
Richter M. 1996. Klimatologische und pflanzenmorphologische Vertikalgradienten in Hochgebirgen. Erdkunde 50, 205-237.
Scheithauer J., Grunewald K., Helle G., Günther B., Gikov A. 2009. Bosnian pine (*Pinus heldreichii*) as geoarchive at the timberline in the Pirin mountains and on the Balkan Peninsula. Biotechnology & Biotechnological Equipment 23, 96-99. 10.1080/13102818.2009.10818374
Schroeder F.-G. 1998. Lehrbuch der Pflanzengeographie. Wiesbaden.
Schreiber H.J. 1998. Waldgrenznahe Buchenwälder und Grasländer des Falakron und Pangäon in Nordostgriechenland. – Dissertation Universität Münster. Arb. Inst. Landschaftsökologie, 4.
Schweingruber F.H. 1993. Trees and Wood in Dendrochronology. Springer-Verlag Berlin Heidelberg, VII +402 pp.
Schütt P. 1994. Tannenarten Europas und Kleinasiens. Ecomed, Landsberg am Lech, Germany, 132 pp.
Sidiropoulou A., Chouvardas D., Mantzanas K., Stefanidis S., Karatassiou M. 2022. Impact of transhumant livestock grazing abandonment on pseudo-alpine grasslands in Greece in the context of climatic change. Land 11, 2126. https://doi.org/10.3390/land11122126
Slatyer R.O., Noble I.R. 1992. Dynamics of montane treelines. In: Hansen A.J., Di Castri F. (Eds.). Landscape boundaries – Consequences for Biotic Diversity and Ecological Flows. (=Ecological studies, Vol. 92). New York, USA, 346-359.
Spanos K.A., Skouteri A., Gaitanis D., Petrakis P.V., Meliadis I., Michopoulos P., Solomou A., Koulelis P., Abramidou E.V. 2021. Forests of Greece. Their multiple functions and uses, sustainable management and biodiversity conservation in face of climate change. Open Journal of Ecology 11, 374-406. https://doi.org/10.4236/oje.2021.114026
Stevanović V., Tan K., Iatrou G. 2003. Distribution of the endemic Balkan flora on serpentine I. – obligate serpentine endemics. Plant Systematics and Evolution 242, 149–170. https://doi.org/10.1007/s00606-003-0044-8
Strid A. (Ed.) 1986. Mountain flora of Greece, Vol. 1. Cambridge: Cambridge University Press, xxx + 822 pp.
Strid A. 1995. The Greek mountain flora, with special reference to the Central European element. Bocconea 5, 99-112.
Strid A., Tan K. (Eds.) 1996. Flora and vegetation of the Peloponnese and Kithira. Copenhagen, Botanical Institute, pp. 991 + appendix 24 pp.
Thanos C.A., Marcou S., Christodoulakis D., Yannitsaros A. 1989. Early post-fire regeneration in *Pinus brutia* forest ecosystems of Samos island (Greece). Acta Oecologica/Oecologia Plantarum 10, 79–94.
Thirgood J.V. 1981. Man and the Mediterranean forest. London and New York: Academic Press, x + 194 pp.
Touchan R, Xoplaki E., Funkhauser G., Luterbacher J., Hughes M., Erkan N., Akkemik U., Stephan J. 2005. Reconstructions of spring/summer precipitation for the Eastern Mediter-

ranean from tree-ring widths and its connection to large-scale atmospheric circulation. Climate Dynamics 25, 75-98. https://doi.org/10.1007/s00382-005-0016-5

Tranquillini W. 1979. Physiological ecology of the alpine timberline. Springer-Verlag, Berlin:. 137 pp.

Vitali A., Garbarino M., Camarero J.J., Malandra F., Toromani E., Spalevic V., Curovic M., Urbinati C. 2019. Pine recolonization dynamics in Mediterranean human-disturbed treeline ecotones. Forest Ecology and Management 435, 28-37. https://doi.org/10.1016/j.foreco.2018.12.039.

Voliotis D. 1976. Die Gehölzvegetation und die Vegetationszonierung des nordgriechischen Gebirgszuges Voras-Vermion-Pieria-Olymp-Ossa. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 97(1), 120-154.

Walter H. 1975. Betrachtungen zur Höhenstufenfolge im Mediterrangebiet (insbesondere Griechenland) in Verbindung mit dem Wettbewerbsfaktor. In: Dafis S., Landolt E. (Eds.). Zur Vegetation und Flora von Griechenland, 72-83.

Wieser G., Matyssek R., Luzian R., Zwerger P., Pindur P., Oberhuber W., Gruber A. 2009. Effects of atmospheric and climate change at the timberline of the Central European Alps. Annals of Forest Science 66, 402. https://doi.org/10.1051/forest/2009023

Xoplaki E., Maheras P., Luterbacher J. 2001. Variability of climate in Meridional Balkans during the periods 1675-1715 and 1780-1830 and its impact on human life. Climatic Change 48, 581-615

Xystrakis F., Theodoropoulos K., Eleftheriadou E., Reif A. 2006. The vegetation of forest and shrubland with creeping *Pinus heldreichii* in" Elikodromio", Olympus National Park, Greece. Plant ecology. Vegetation and habitat diversity. Proceedings of the IV Balkan Botanical Congress, Sofia, 347-354.

Zindros A., Radoglou K., Milios E., Kitikidou K. 2020. Tree line shift in the Olympus Mountains (Greece) and Climate Change. Forests 11, 985. https://doi:10.3390/f11090985